

WINTER DOMINANCE RELATIONSHIP IN BLACK-CAPPED CHICKADEES

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DOMINANCE relationships for flocks of birds have been found to vary around two main types. Schelderup-Ebbe recognized individuals within flocks, utilizing marked chickens (*Gallus gallus*), and discovered they were organized into a "peck-right" unilateral despotism, in which the top bird pecks all, the second dominates all but the top one, and so on; the bottom bird pecks none. Similarly, within flocks of pigeons (*Columba livia*) Masure and Allee (1934) described "peck-dominance" organization which was less rigid than in domestic fowl. Individuals of this species pecked one another; however, the dominant birds pecked more and were pecked less than subordinates. Dixon demonstrated peck-right organization within wild flocks of Mountain Chickadees (*Parus gambeli*) (1965) and Carolina Chickadees (*P. carolinensis*) (1963). Due to conflicting descriptions in the literature, the winter flock behavior of Black-capped Chickadees (*P. atricapillus*) is not clear in regard to dominance relationships. Odum (1942) left the status of intermediate members in flocks undetermined, whereas Hamerstrom (1942), also working with Blackcaps, found the dominance order of any two birds was clear, but attempts to arrange the flock as a whole failed. Brewer (1961) concluded that in small flocks of Carolina and Black-capped Chickadees dominance relationships were linear, while in "larger assemblages" deviations from complete linearity occurred. The presence of a dominance hierarchy and the fact that closely related species of the genus *Parus* (Dixon, 1963; 1965) do show winter range defense, suggest that Black-capped Chickadees may also exhibit this behavior. The present paper reports observations of the social organization of Black-capped Chickadees to help clarify their winter dominance relationships.

METHODS

To attract chickadees for trapping, banding, and behavioral observations, continuously baited feeding stations were set in late December, 1967, in a small river bottom woods of approximately 35 acres located 2.5 miles north of Mankato, Minnesota (Fig. 1). The birds were trapped, fitted with a Fish and Wildlife band, and color-marked (Magic Marker on body plumage and Testor's airplane dope on retrices). Observations were carried out over the entire study area; however, the bulk of the data was collected at the five feeders. Criteria for dominance-subordination used in this study were similar to those used by Dixon (1965): (1) successful or unsuccessful attempts at displacement from a perch or food, (2) withdrawal upon detection of an approaching bird, (3) obvious waiting of an individual until another had finished its feeding and departed. Dominance-

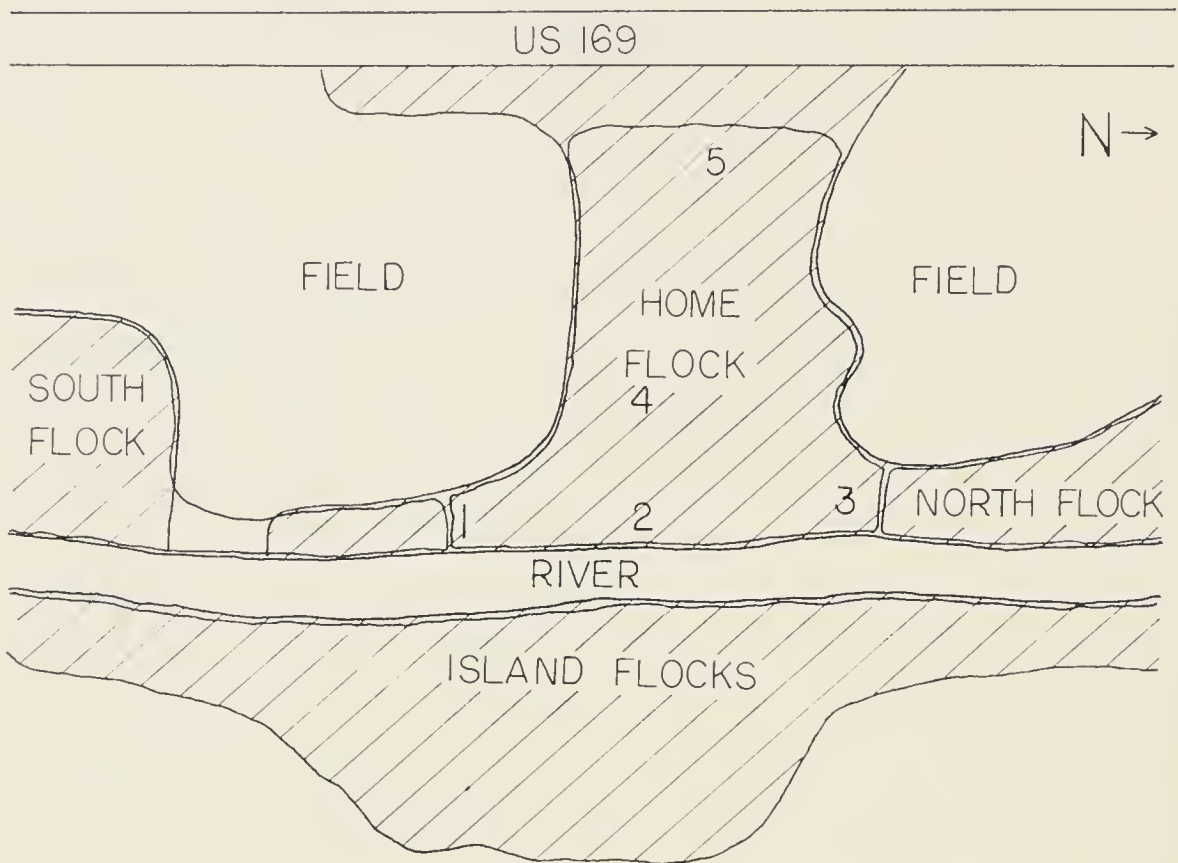


FIG. 1. Map of the study area showing disposition of winter flock ranges, feeding stations 1-5, and association with plowed fields, Minnesota River, highway, and woods (denoted by diagonal lines).

subordination activities were recorded through January and February, 1968. Flock range and composition were ascertained by observations while following the flocks and noting where individuals were seen throughout the study. Attempts were made to arrange individuals within flocks into hierarchies of dominance on the basis of wins and losses at the feeders. If any two individuals next to each other in a hierarchy had no observed dominance encounters with each other, they were arranged randomly with respect to each other, such as BGT and RRR (Table 1). Additional observations were carried out through March and April to ascertain sex and breeding territories.

RESULTS AND DISCUSSION

Flock composition and winter range.—Indications were that the local chickadee population and flock composition varied during the winter. After the initial capture of 20 chickadees from 30 December 1967 to 4 January 1968, no new birds were observed until 29 January when 18 new birds were captured during February. Of the total 38 captured, 7 early captures were members of the home flock; the 18 new captures constituted the south flock, and the remainder were members of the north and island flocks (Fig. 1). The most extensively studied of these flocks, the home flock, occupied a well-defined

winter range of approximately 35 acres. Because of much wandering and trespassing, the winter ranges of the other 3 flocks were not clearly defined. The home flock was almost always in their winter range and generally traveled together, although not all members were always present at any given time. The other flocks, however, were less cohesive and the composition varied so much that much of the time they could not be identified and followed as flocks. Members of other flocks frequently visited the home flock range, especially near the river boundary, and members of the home flock were observed on several occasions to fly across to the island. Odum's (1942) flocks in New York varied in composition, and his average flock range was 35 acres. In Massachusetts, the winter flock range was established in the fall and retained with only minor changes until spring dispersal (Wallace, 1941). In Utah, the Black-capped Chickadee (M. Frydendall, pers. comm.) occupied restricted flock territories of 6 to 8 acres, and the flock composition was stable throughout the winter. It is apparent that flock behavior in Black-capped Chickadees varies. Brewer (1961) emphasized that flock size, as well as degree of constancy of flock composition in chickadees, varies with many factors both of the birds themselves and of the environment.

Intraflock dominance.—Enough gregariousness was present in Black-capped Chickadees so that organized flocking occurred. However, individuals were antagonistic toward each other in that no two birds were ever observed to tolerate each other at close proximity, such as at a 4×8 inch feeder. Intraflock dominance was characterized by a minimum of display, such as posturing, vocalizing, or actual combat; thus, subordinate individuals readily gave up feeders upon approach of a dominant bird and would not challenge dominants at the feeders. During this study a subordinate individual was often observed to withdraw from a feeder when a dominant individual was approaching on the wing at a distance of 10 to 15 yards. In order for such coordination to exist between dominant and subordinate flock-mates, Black-caps must be able to efficiently recognize other individuals. Similar observations were reported by Dixon (1965) in the intraflock dominance contests of Mountain Chickadees.

Within the home flock, individuals were organized into a peck-right dominance hierarchy which held wherever the flock traveled within the flock range. Table 1 summarizes the dominance-subordination data for the members of the home flock. These observations are from five different locations inside the home flock range (feeding stations 1–5, Fig. 1); thus a true peck-right dominance hierarchy existed for this flock of birds because the hierarchy was constant at different locations. Mountain Chickadees (Dixon, 1965) and Carolina Chickadees (Dixon, 1963) also showed a peck-right winter flock organization, but Great Tits (*Parus major*) (Brian, 1949) and Blue Tits

TABLE 1

DOMINANCE-SUBORDINATION RELATIONSHIPS OF THE HOME FLOCK.

Data from all five feeding stations, 2 January to 29 February, 35 days of observation. Winners read horizontally.

	RRR	YTT	GC	BGT	RRF	BRF	RC	Total Wins	% Wins
♂ RRR	—	5	18	8	15	11	7	64	96
YTT	—	—	4	—	9	6	9	28	85
GC	—	—	—	2	2	6	1	11	31
♀ BGT	3	—	—	—	—	3	2	8	44
♂ RRF	—	—	—	—	—	12	6	18	40
BRF	—	—	2	—	1	—	6	9	20
♀ RC	—	—	—	—	—	—	—	0	0

(*P. caeruleus*) (Colquhoun, 1942) both showed social rank in winter flocks dependent on the distance from subsequent breeding territories. Marler (1955) would describe these latter two species as exhibiting peck-dominance because of the effect of location on the dominance outcome. It is necessary that observations from several different locations be used to establish a peck-right hierarchy, because data from a site-dependent, peck-dominant hierarchy, such as in Great Tits, appears to be peck-right if collected from one location only.

Few reversals in the hierarchy occurred during observation (Table 1). On 29 February, the last day the home flock was observed together, the alpha male, RRR, three times allowed BGT to feed while he waited at station 1. However, RRR dominated BGT twice on that day at the same station, and six times prior to this at various stations. Proof of sex was not obtained, but RRR appeared to be a male from his dominance position and role in territory defense in April, 1968, and BGT was his mate (to be further discussed in the spring dispersal section). It appeared that during the winter the male of a pair (RRR) dominated the female (BGT) until near spring dispersal, when he may wait for her to feed. Odum (1942) reports that feeding of the female by the male does not appear in courtship, but occurs later, particularly in incubation. So these reversals of RRR and his mate may be the closest thing to feeding during the early stages of pairing which the Blackcap shows.

Other reversals in the home flock were cases of unexplainable revolts on the part of BRF. Hammerstrom (1942) recorded only one reversal in 76 fights among Blackcaps. However, only actual fights were used as dominance criteria, and the flock as a whole was not arranged into a dominance hierarchy. Odum (1942) called the intermediate birds in his hierarchies "peck-dominant"

because of frequent reversals. The only reversals reported in Carolina or Mountain Chickadees by Dixon (1963, 1965) were the temporary loss of status by mates of alpha males when the males were removed. My study did not indicate high status for the mate of the alpha male; she ranked fourth out of seven. No attempt to remove the alpha male was made in this study.

Spring dispersal.—After traveling together as a fairly cohesive unit during January and February, 1968, the home flock was observed broken up into pairs on 6 March and subsequently never seen again as a unit. Four members of the home flock, RRR, BGT, RRF, and RC, were observed as pairs in the east half of the home flock woods. RRF and RC, fifth and last in the home flock hierarchy respectively, occupied the middle portion of the home flock range next to the river and were observed as a pair 15 March, 2 April, and 21 April. When seen together RRF appeared to be the male from his singing and general aggressiveness. Dixon found alpha males, but no individuals low in the hierarchies, of most winter flocks remained to establish pair territories within the flock range in Carolina Chickadees (1963) and Mountain Chickadees (1965). RRR and BGT, first and fourth in the home flock hierarchy respectively, occupied the central portion of the home flock woods and were observed together 6 March and 21 April. On 21 April, while their mates fed nearby in the home flock woods, RRR actively directed the “*phoebe*” territorial song of the Blackcap at RRF, who actively replied. This singing duel lasted for nearly 30 minutes, and is further evidence that RRR and RRF were males and RC and BGT females. Of the other home flock members only YTT, second in the hierarchy, was subsequently observed after dispersal, on 6 March and 15 March, foraging in the strip of trees beside the highway, approximately 300 yards from the home flock winter range.

Interflock dominance.—Dominance between flocks of Black-capped Chickadees was less well defined than that within the home flock. Members of the home flock did not challenge trespassing birds on the border of the home flock range, except RRR and RRF, both thought to be males who were known to have remained in the winter range and established territories. These two males actively challenged two dominant birds from the south flock. Late in February, RRR and RRF went through extensive posturing, calling, chasing, and actual physical combat with two intruders on the border between the home flock and south flock winter ranges at feeder 1 (Fig. 1). In these encounters RRR and RRF of the home flock were dominant in all instances except one, when, after a long display and chase, RRR was displaced by a dominant individual of the south flock. These interflock displays were much more violent than the few timid challenges within the home flock. The other members of the home flock were dominant over intruders at the feeders (Table 2) but did not actively challenge or chase any of them. Similar

TABLE 2

INTERFLOCK DOMINANCE-SUBORDINATION ENCOUNTERS OF THE HOME FLOCK.

Data from all intruders over the entire home flock range from 2 January to 29 February, 35 days of observation.

	Wins	Losses	Total	Per cent Won
♂ RRR	28	1	29	97
YTT	22	0	22	100
GC	15	1	16	94
♀ BGT	1	2	3	33
♂ RRF	25	1	26	96
BRF	9	4	13	69
♀ RC	20	5	25	80
Total	120	14	134	90

relationships were found between intraflock and interflock encounters in Mountain Chickadees (Dixon, 1965). One important difference does exist, however: in the Mountain Chickadee the alpha males directed hostilities against all intruders, while in this study the Blackcap alpha male actively challenged only dominant intruders, even though he dominated all at the feeders. An even better perceptual system than in intraflock dominance is indicated here, for all home flock members recognized intruders and RRR and RRF recognized the dominant individuals of the south flock.

The birds of the south flock singled out for attack by RRR and RRF were ALLG and WTBS, who won 75 and 100 per cent, respectively, of their dominance encounters with flock mates. This evidence strongly suggests that ALLG and WTBS were dominant members of the south flock (compare with percentage won of RRR and YTT of the home flock, Table 1). Because of the south flock's late appearance and my difficulty in establishing feeding stations in the south flock woods, sufficient data to arrange the entire flock into a hierarchy are lacking. I suspect that ALLG and WTBS were males and that they established or intended to establish pair territories in the general area of feeder 1, but attempts to locate these and to ascertain their sex failed. WTBS was seen after spring dispersal near station 1 on 6 March 1968.

Because active conflict and interflock dominance appeared to be related to the location of the subsequent breeding territories of the home flock males, Blackcap interflock behavior fits the concept of peck-dominance as modified by Allee (1942) to include the location of the contests. Therefore, Black-capped Chickadees had a system of peck-dominance organization working between flocks, simultaneously with a peck-right system within the flock, similar to the Mountain Chickadee (Dixon, 1965).

With the exception of BGT, the individuals who remained in the winter flock range to establish breeding territories (RRR, RRF, RC) had unusually high numbers of interflock encounters. The males of this group also won more interflock encounters than any other home flock members. Members of the home flock were in general dominant over trespassing birds, winning 90 per cent of all interflock contests observed within the home flock range. Thus all the members of the home flock, whether high or low in the hierarchy, whether or not they established later pair territories within the home flock range, had the advantage of precedence to food over intruders within the home flock range.

The dominance position of an individual within the home flock had an important relationship to its success in interflock contests (Table 2). The alpha male, RRR, had and won more interflock contests than any other bird, while the bottom two birds, RC and BRF, lost more contests than any other birds. However, they still won most encounters at the feeders. The per cent won column of Table 2 shows a trend of decrease down the hierarchy; the average of the top three individuals is 97 per cent while the average of the bottom three is 82 per cent.

Because only RRR and RRF, and not the flock as a whole, actively excluded trespassers from the flock boundary, the concept of a "winter flock territory" does not apply to this species. Odum (1942) uses winter flock range instead, and Dixon (1963) found that Carolina Chickadees did not exhibit group territories, because only the alpha male defended the area against males of other flocks. Thus a "group territory" existed only for the dominant males who remained to nest in the winter range. The remainder joined the dominant males to form the winter flock, but played no noticeable part in winter range defense.

SUMMARY

The winter flock behavior of Black-capped Chickadees was studied in relationship to their dominance hierarchy. Within the home flock a peck-right dominance hierarchy was described, but between flocks dominance relationships were better characterized as peck-dominant. The intolerance of the home flock males to dominant members of other flocks was associated with the location of subsequent breeding territories within the winter range, while the intraflock dominance hierarchy held wherever the flock traveled. Dominance-subordination within the home flock involved little calling, posturing, and no chasing, while interflock encounters did when they involved dominant males.

Observations suggested that individual variability is important in interpreting the behavior of this species. One flock of seven chickadees, the home flock, moved around its winter range with little internal conflict; trespass of subordinate members of neighboring flocks was common, but the visiting birds were subordinate to the residents at the feeders. Dominant individuals of other flocks did not trespass deep into the home flock winter range, but remained on the periphery where they were challenged by dominant

home flock males. The surrounding flocks varied in size from 4 to 18 individuals, were less cohesive, and could not be located at any specified time as could the home flock.

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